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TEXAS MEMORIAL MUSEUM

FOSSIL VERTEBRATES
FROM MILLER'S CAVE
LLANO COUNTY, TEXAS

by

Thomas Hudson Patton

THE UNIVERSITY OF TEXAS

24TH AND TRINITY • AUSTIN 5, TEXAS

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Introduction

In the last twenty years research in vertebrate paleontology, especially that dealing with paleoecology and zoogeography, has led to a greater insight into the biological and meteorological effects of the successive glaciations during the Pleistocene. The extensive Pleistocene deposits of western North America and their abundant vertebrate faunas have provided a rich source of material for such research. The fauna described in this paper, and the inferences drawn therefrom, are intended to reveal a small portion of the history of the Pleistocene in the southwestern United States.

In the spring of 1960 Mr. Thomas Warden, while prospecting for deposits of bat guano, noticed bone fragments of small animals in the sediment of a dry cave near Llano, Texas. He subsequently reported his find to the Vertebrate Paleontology Laboratory at The University of Texas, and a trip was made to the cave to explore the possibility of its excavation. Fossil bones were so numerous that excavation of the cave and description of its contained fauna were made the subject of the writer's master's thesis at The University of Texas. Excavation was carried out by the writer during August, 1960, and the following school year.

Regional Geology

The Llano region of central Texas includes a topographic basin in which rocks of pre-Cambrian age are exposed and a surrounding higher area of Paleozoic and Cretaceous rocks forming a dissected plateau. From the center of the basin a broad rolling plain may be seen stretching in all directions, interrupted occasionally by hills and encircled by a scarp of Paleozoic rocks. The central basin is eroded on granite, gneiss, and schist, which here are less resistant than the Paleozoic strata which form the rim of the basin.

Miller's Cave is located in the Riley Mountains, thirteen miles southeast of the town of Llano, Llano County, Texas. Riley Mountain proper forms a table-like mass about 15 miles long and several miles across and stands well

above the surrounding country. It is supported by very gently dipping Cambrian strata. The Ellenburger limestone (Ordovician) lies immediately above the Cambrian beds and is found at the crest of the Paleozoic scarp except where faulting has disturbed this relation. Although the Ellenburger is primarily a sublithographic limestone, it contains considerable quantities of dolomite and chert. Miller's Cave is formed within the Ellenburger limestone.

The cave opens on the north side of a hill overlooking Honey Creek just south of Dancer Flats. The entrance is in a clump of trees about 115 feet up the hill at an elevation of approximately 1350 feet (Figs. 1, 2).

Climate

The climate of the Llano region is semiarid, the average precipitation amounting to approximately 20 inches per year. Rainfall varies considerably from one year to the next and is very unevenly distributed throughout the seasons. It is not uncommon for one third of the annual rainfall to come in a single week or to have periods of drought lasting for 12 to 15 weeks. Usually most of the rain comes in spring and fall; the summers are dry and hot. The mean annual temperature is about 70.5° F. The daytime winter temperature from No-

vember to April ranges from 40 to 70° F. Summer days are hot, with the daytime temperature ranging from 80 to 110° F. and averaging nearly 90°. Seasonal extremes range from -7 to 115° F. (Texas Almanac, 1958-59).

According to Thornthwaite (1948), who classified climate on the basis of the interrelationships between temperature, precipitation, and evapotranspiration, the Llano region today has a semiarid climate belonging to the third mesothermal with little or no water surplus in any season (DB₃'db₄).



Fig. 1. Southwest corner of topographic map of Llano County, Texas (after Paige, 1912). X marks location of Miller's Cave. Scale: one inch equals 5.2 miles. Contour Interval: 25 feet.

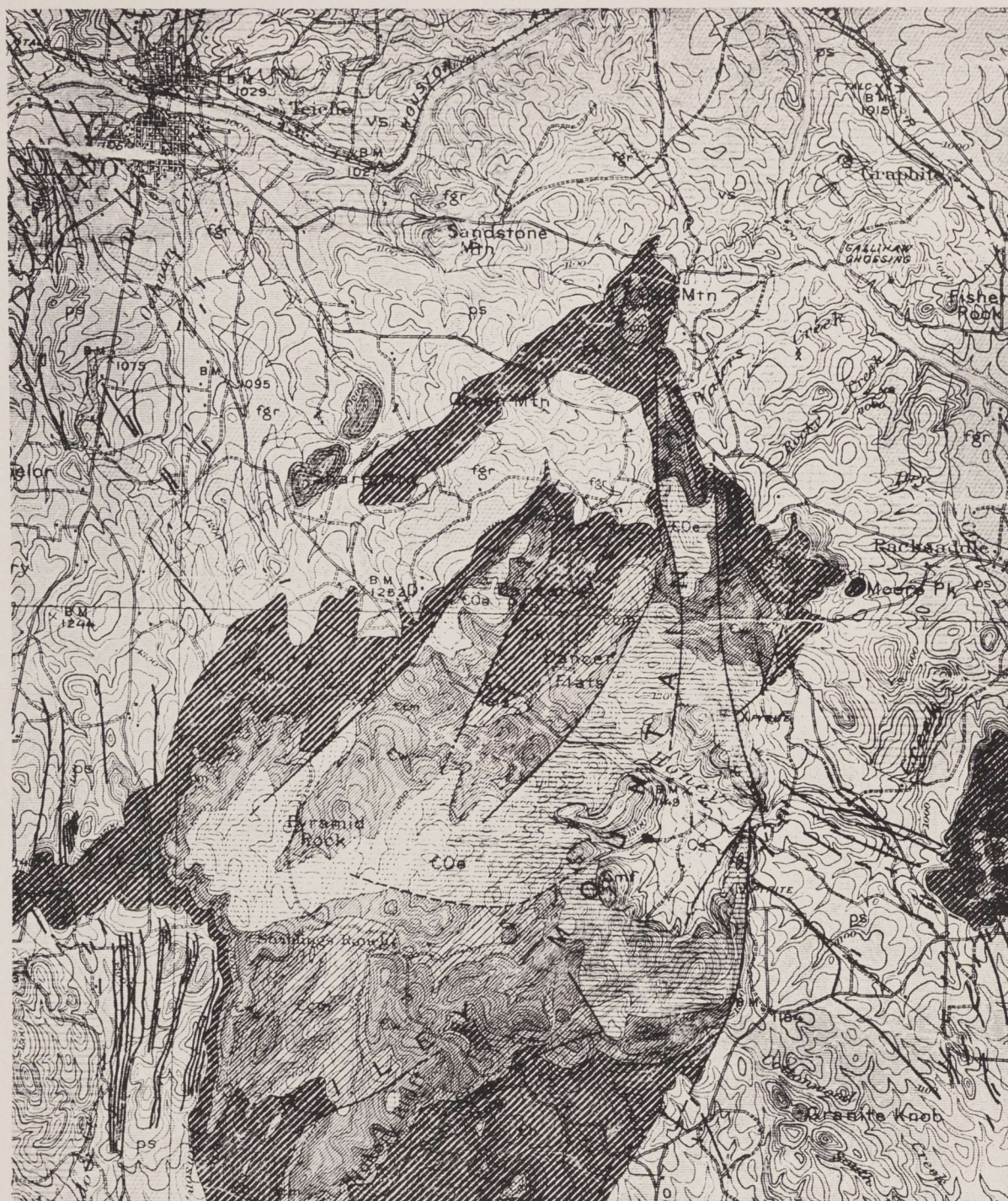


Fig. 2. Southwest corner of geologic map of Llano County, Texas (after Paige, 1912).

Biota

Blair (1950) recognizes seven biotic provinces within the state of Texas, distinguishable by their respective ecological associations (Fig. 3). The Austroriparian province extends into eastern Texas and occupies a strip of coastal plain from the Gulf of Mexico to the Ouachita Mountains of Oklahoma. The plants and animals of this province are mostly species that extend eastward on the coastal plain to the Atlantic. The Texan province, bordering the Austroriparian in eastern Texas, is a broad

ecotone between the Austroriparian forest and semiarid grasslands to the west. It is characterized by the interdigitation of forest and grassland associations and species. The Tamaulipan provinces includes the Gulf coastal plain south of the Balcones Escarpment and west to the boundary between ped-
alfer and pedocal soils. This province is characterized by the intermixture of Neotropical species, Austroriparian species and southwestern desert species. The Chihuahuan province

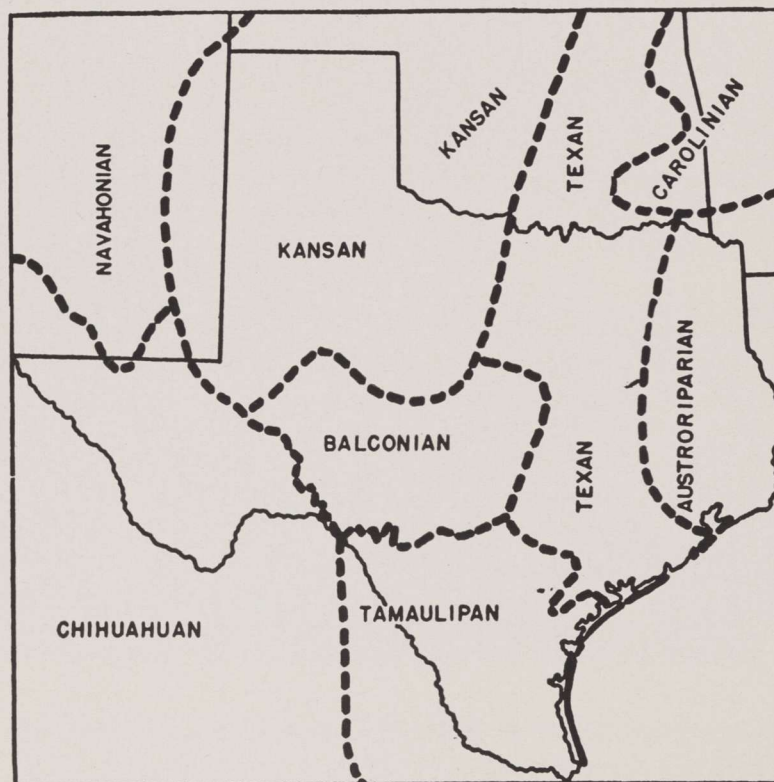


Fig. 3. The biotic provinces of Texas, after Blair (1950).

includes all of Trans-Pecos Texas except the Guadalupe Mountains. The plants and animals of this province are mostly species that are widely distributed in the mountains and deserts of southwestern North America. The Navahonian province, which includes a large part of New Mexico, extends into Texas in the Guadalupe Mountains. The fauna shows close relationship to the fauna of the Chihuahuan province, but several high-elevation species occur in the Navahonian and fail to reach the Chihuahuan. The Kansan province takes in the Panhandle and the red plains to the east of the escarpment of the high plains. The plants and animals are mostly grassland species, but some Austroriparian species extend along wooded stream valleys into the eastern part of the province. The Balconian province includes the Edwards Plateau, the Lampasas Cut Plain, and the Llano Uplift Region. This is a region of intermediate ecological conditions between the eastern forests and the western deserts (Blair, 1950, p. 115).

According to this classification, the Miller's Cave region today belongs to the Balconian biotic province. The fauna is a mixture of Austroriparian, Tamaulipan, Chihuahuan, and Kansan province species. The Balconian province includes such species as *Bassaricus astutus*, *Conepatus mesoleucus*, *Citellus variegatus*, *Peromyscus pectoralis*, *Neotoma albigula*

(Chihuahuan); *Didelphis virginiana*, *Sciurus niger*, *Sylvilagus floridanus*, (Austroriparian); *Tayassu angulatum*, *Dasypus novemcinctus*, *Citellus mexicanus* (Tamaulipan); *Taxidea taxus*, and *Reithrodontomys montanus* (Kansan). Other common forms include *Perognathus hispidus*, *Sigmodon hispidus* and *Lepus californicus*.

Tharp (1939) describes three vegetational regions within the Balconian province (Fig. 4.) His oak-hickory-mesquite region includes the Llano Uplift. The Llano region and adjacent parts of the Edwards Plateau are for the most part more thickly wooded than the plains country to the north, west, and south. Mexican cedar (*Juniperus mexicana*) is abundant in limestone areas, especially in the eastern part of the region. Scrubby oaks (*Quercus texana* and *Q. virginiana*) are abundant on sandstone and granite, while mesquite (*Prosopis juliflora*) and various spiny bushes characterize areas underlain by argillaceous and schistose rocks. Two kinds of cactus (*Opuntia lindheimeri* and *Echinocactus texensis*) occur in the area, as do yucca and various spiny bushes of the semiarid types. The floodplains of the larger streams support a good growth of large live oaks (*Quercus virginiana*), pecans, (*Carya illinoensis*), elms (*Ulmus americana*, *U. crassifolia*), and hackberries (*Celtis occidentalis*).

Description of Cave

Miller's Cave is divided into two rather distinct chambers, north and south, the long axes of which intersect to form an open V. There is little constriction of the walls at this point. The chambers are broad, open, and symmetrical, and are approximately 180 feet in combined

length. The cave ranges in width from 20 to 60 feet, and averages about 20 feet from floor to ceiling (Fig. 5).

Access to the cave is gained through a shaft in a breccia formed by collapse of part of the roof. The debris from this collapse forms a

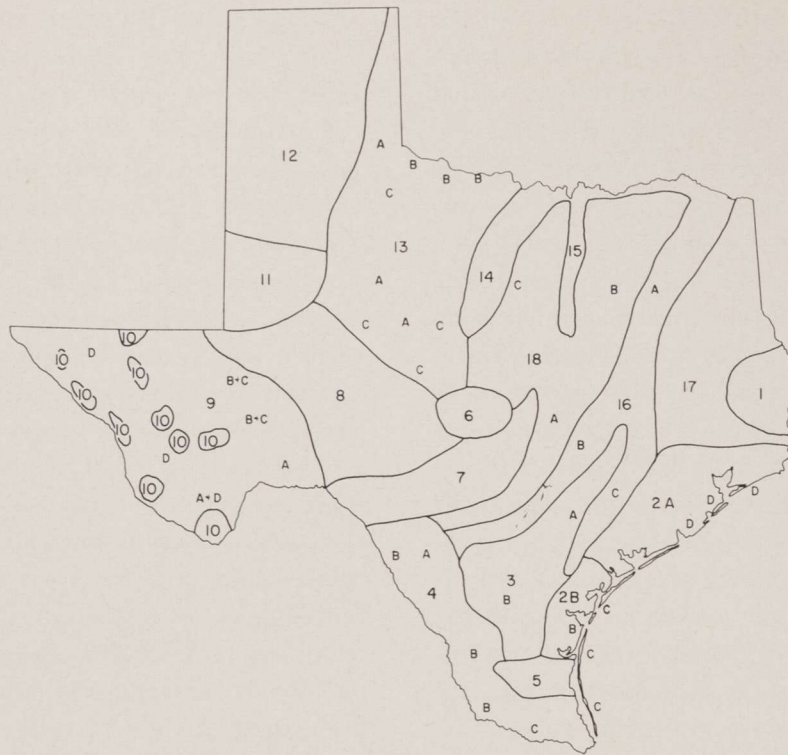


Fig. 4. Vegetational provinces of Texas, after Tharp (1939).

- | | |
|---|---------------------------------------|
| 1. Long-leaf Pine | A. Sotol-Lechuguilla Foothills |
| 2. Coastal Prairie | B. Mesas |
| A. Upper coast south to San Antonio Bay | C. Intermesa Valley Flats |
| B. Lower coast north to San Antonio Bay | D. Intermountain Valleys |
| C. Insular Dunes | 10. Mountain Forests and Oak-Savanna |
| D. Marshes | 11. Sandy South Plains |
| 3. Fayette Prairie and Transition Zone | 12. High Plains |
| A. Fayette Prairie | 13. Mesquite Savanna |
| B. Transition Zone between Fayette Prairie and Mesquite-Chaparral | A. Gently rolling and sandy |
| 4. Mesquite-Chaparral | B. Red River dunes |
| A. Uvalde-Carrizo Springs (Winter Garden Area) | C. Bold rocky hills |
| B. Hilly "Brush Country" | 14. Western Cross Timbers |
| C. Lower Rio Grande Valley | 15. Eastern Cross Timbers |
| 5. Mainland Dunes | 16. Oak-Hickory |
| 6. Oak-Hickory-Mesquite of the Igneous Central Mineral Region | A. Northeastward from Brazos River |
| 7. Oak-Juniper of Hilly Marginal Portion of Edwards Plateau | B. Northwestward from Fayette Prairie |
| 8. Live-oak-Mesquite Savanna | C. Southeastward from Fayette Prairie |
| 9. Foothills and Mesa Region westward from Pecos River | 17. Mixed Pine-Oak |
| | 18. Blackland Prairie |
| | A. Southwestward from Brazos River |
| | B. Eastward from Cross Timbers (E) |
| | C. Westward from Cross Timbers (E) |

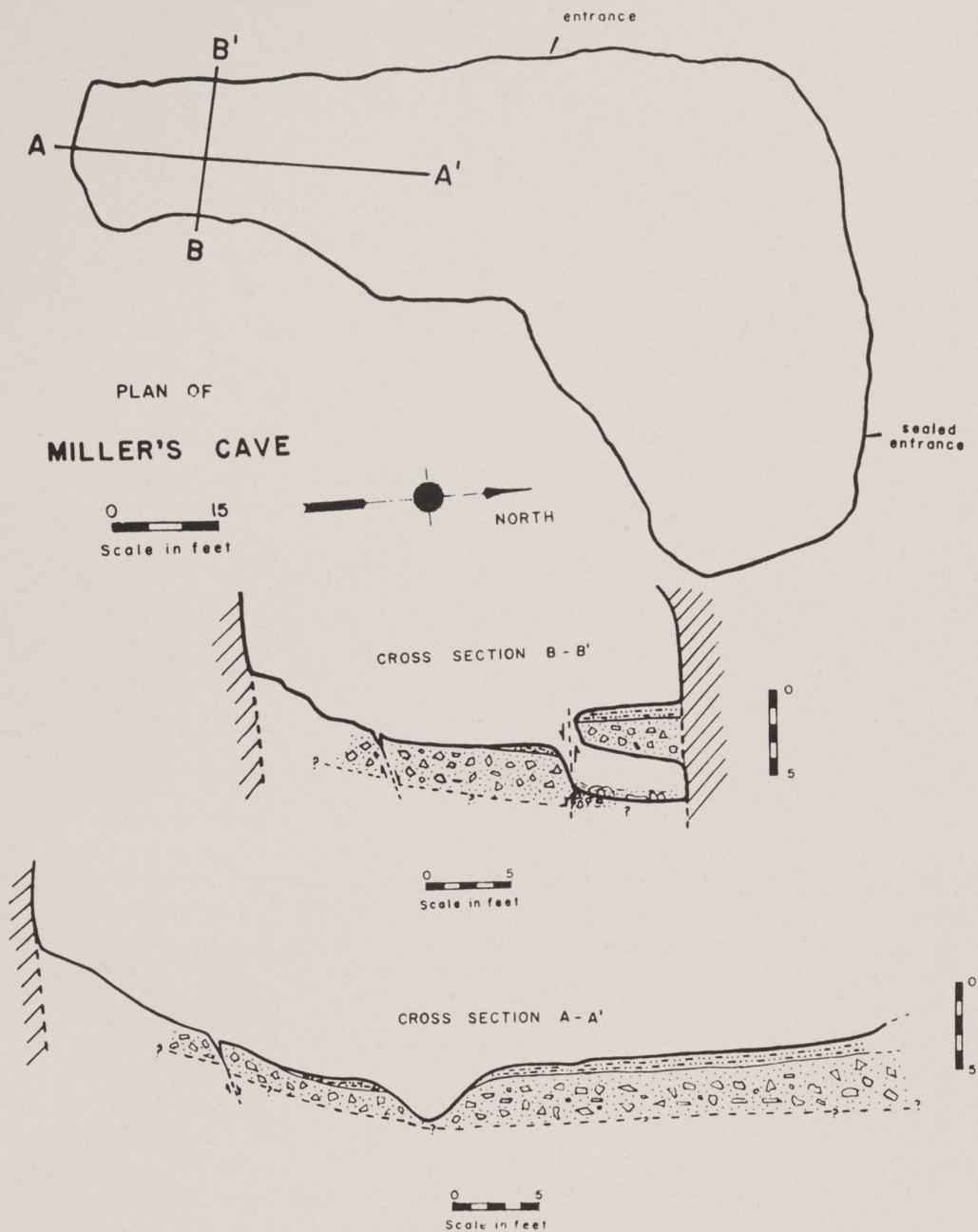


Fig. 5. Plan of Miller's Cave, showing longitudinal and transverse cross-sections of the south chamber.

large portion of the talus fan, or debris cone, radiating from the entrance. From its apex at the entrance the fan dips rather steeply for approximately 40 feet where it grades into a level floor of more or less horizontal layers of sedi-

ment. The fan is situated at the junction of the two chambers. In the southeastern corner of the north chamber there is a second talus fan, now sealed off from the outside. (Fig. 6C)

The north chamber is smooth and uniform.



Fig. 6A



Fig. 6B



Fig. 6C

Fig. 6. Interior of Miller's Cave. A. View of south chamber. B. Bone-bearing travertine ledge in south chamber. C. View of north chamber, showing extinct cone debris.

With the exception of one wall cavity opening at floor level in the northwest corner, the walls of the chamber are devoid of much pocketing or gross irregularities. Large flowstone and dripstone features are absent. Against the west wall of the chamber occur a series of small travertine dams, partially filled with water.

Features of the south chamber of Miller's Cave differ considerably from those of the north (Fig. 6A). Two large blocky stalagmitic structures jut up from the floor of the cham-

ber, while the east wall is almost completely blanketed by flowstone. In the east wall a large joint-controlled cavity extends obliquely upward for about 20 feet and then terminates blindly. Smaller shafts and chimneys occur in the south wall, and although they cannot be followed, it appears that they are now blocked off from the outside. There is a short series of travertine dams at the base of the south wall. Perhaps the most striking feature of the chamber is a hard semi-circular ledge projecting

from the cave walls. (Fig. 6B) This ledge was formed by collapse of a travertine-cemented sedimentary unit which originally extended across the entire chamber. The large slump block dips sharply from its hinge on the east ledge and disappears under younger sediment near the west ledge where there is a throw of

some three feet. Erosion of the sediment which once lay beneath the travertine layer has resulted in the formation of a large cavity under the west ledge. Except where dripping is concentrated, practically the entire surface of the cave floor is covered with varying thicknesses of guano deposits.

Sedimentation

Most of the cave sediments are derived from soil material weathered out and transported from the surface. The manner in which sediment is introduced to caves varies, but in dry caves it passes primarily through spring outlets and through shafts or chimneys reaching up to the surface. Sediment in Miller's Cave has entered in this fashion. In the previous section the presence of talus fans was noted. It is readily apparent that most of the cave sediment has passed over the talus fan, regardless of the distance from the entrance. This must be qualified to the extent that there are secondary sources, as mentioned above, which have provided sediments from a direction opposite that of the principal talus fan. Such evidence as original dip of the sedimentary layers and imbrication of included particles were valuable in determining variation in direction of source in Miller's Cave.

Because most of the sedimentary material dropped or was washed into the cave from the surface slope above the cave entrance, it is of essentially the same composition as the weathered soil on the outside (CLAY MINERALOGY, p. 19).

The inactive talus fan in the north chamber closely approaches the presently active one, and it is possible that sedimentation from the

two entrances was once concurrent. Visual inspection of the sediments in the wall of a trench dug between the fans revealed no evidence of interdigitation or any other feature indicating direction of source. This is in part because of the general coarseness of cave sedimentation, the large size of much of the sedimentary material, and in part because the sediments were derived from the same source material and are consequently indistinguishable.

The south chamber has received most of its sediment from the present entrance. A smaller quantity of sediment in this chamber apparently was washed in from the surface through narrow chimneys in the ceiling and walls of the cave, but very little, if any, seems to have been derived from the extinct fan in the north chamber. Sediments in the north chamber were derived from the inactive fan and from the active one at the junction of the chambers. It was not possible to determine the relative amount of material introduced to the north chamber through each entrance. There is no evidence that sediment in the north chamber passed through any openings other than the now sealed entrance.

Material formed from surface weathering of the parent limestone constitutes the largest

portion of the finer grained sediments in the cave, although clayey residua of impure limestone and dolomite may be important. Much of the larger material is autochthonous, i.e., are fragments of speleothems, breakdown boulders, and cobbles, and insoluble residues of the

parent rock. This last constituent is primarily chert. Calcareous sinter, or travertine, is common in the cave and occurs in the form of dripstone and flowstone. It also comprises a relatively large fraction of a particular stratigraphic unit.

Stratigraphy

Sedimentation in Miller's Cave has varied greatly from one chamber to the other, so that stratigraphic units present in the south chamber are completely absent in the north, and vice versa. Considering the fact that the sediments have been derived from two separate talus cones, one entirely within the north chamber and the other situated at the junction of the two chambers, such a disparity between stratigraphic sequences should not be unexpected. Because the sequences in the two chambers are so different, they will be treated separately.

North Chamber

Sediments in the north chamber were derived from two major sources: primarily from the extinct talus cone in the northeast corner of the chamber, and secondarily from the presently active cone at the entrance.

Two units are recognized: the lowermost unit in this chamber consists almost entirely of limestone rubble which in turn is composed of a mixture of both autochthonous breakdown material and weathering products from the outside. Finer material becomes more abundant towards the top of the unit. Four feet of this unit have been excavated; because digging had to be stopped, its total thickness is undetermined.

Above this rubble unit and separated from it by a transitional contact occurs a loose black clay unit, about two feet thick. The clay appears to be predominantly material which was washed in from the outside. Intermixed with the clay are large quantities of guano. Fresh guano also forms a thick covering over much of the floor of the north chamber.

Sediments in the north chamber are practically barren of fossils. Possibly during the time of accumulation of north chamber sediments, the entrance was too restricted to allow unhindered passage of all but the smallest animals. Predators such as owls, which apparently account for most of the small animal remains in the cave, were unable to utilize the cave so that only those animals that crawled in and died, or whose skeletons were washed in from the slope outside left behind their remains. Bats were then abundant and their skeletal elements comprise the vast majority of what bone material is present.

South Chamber

The fossils were excavated principally from two distinct stratigraphic units occurring in the south chamber: a lower cemented "travertine" unit, and an upper soft brown clay unit (Figs. 5 and 7). Sediments below the travertine are a heterogeneous mixture of clay with



Fig. 7. Photograph of the travertine-supported ledge extending from the west wall of the south chamber. The dashed line marks the contact between the lower travertine unit and the upper brown clay unit.

cobbles and boulders of both limestone and chert. Because they have yielded so little fossil material, they will not be included in this discussion.

Travertine: The travertine unit is a tan to dark brown clay-silt breccia, containing numerous large fragments of angular autochthonous limestone, smaller amounts of surface-derived limestone cobbles and great quantities of fossil bone material. Most of this unit has been very tightly cemented by travertine, or flowstone, precipitated from ground water which seeped through the cave walls and thoroughly soaked the sediments. Although most of the sediments comprising the smaller fraction were derived from the surface, a considerable quantity of material was formed within

the cave. These include insoluble fragments, such as chert, left behind as a by-product of corrosion of the parent rock, angular limestone debris loosened by congelifraction (frost-splitting) from cave portals, and insoluble clay limestone and dolomitic limestone.

Kukla and Lozek (1958) state that travertine beds, which are common in cave profiles, usually "indicate the weakening or complete interruption of the transport of the material from the surface." Further, they state that such beds serve as good indicators of warmer and more humid climatic phases, although they may accumulate during cold periods as well if the rainfall is sufficiently high. Rainfall, therefore, is the critical factor. Lais (1941) studied the size and proportion of limestone debris in

Quaternary cave profiles and discovered that there exists a close dependence of these factors upon the climatic cycle (Kukla and Lozek, 1958, p. 68). The presence of large, angular, unweathered breakdown debris can be correlated with a general increase in regional rainfall, resulting in an increase in the circulation of ground water. The introduction of more ground water into the cave complex would result not only in the precipitation of calcium carbonate in the form of travertine, but would also increase the breakdown process.

Brown Clay: Above the travertine unit in most places is a loose, reddish-brown clay-silt conglomerate, which was originally given the name "clay" because of its unctuous character when wet. This unit contains a much smaller fraction of material larger than coarse sand. Cobbles and boulders, which are so distinctive a part of the underlying travertine unit, have diminished both in number and size. Angularity of the larger components has greatly decreased, while surface weathering features such as pitting, zoning, and staining become

characteristic. The larger material was apparently introduced from the outside rather than being autochthonous breakdown debris. The fossil bone fraction has also become greatly reduced. It appears that conditions at the time brown clay was accumulating differed greatly from those during travertine formation. The large amount of moisture introduced into the cave complex diminished, causing a cessation of travertine deposition as well as reducing the amount of breakdown and corrosion in the walls and ceiling of the cave. Fossils continue to appear in some abundance, but their numbers are sharply cut. It seems possible that the environmental conditions so favorable to the large and diverse fauna of travertine time were altered to the extent that some ecological niches were eliminated, resulting in extirpation of their associated species. Those species which did not disappear altogether were unable to maintain their previously high population density in an increasingly hostile environment.

Clay Mineralogy

Material carried into the cave from the outside bears evidence of surface weathering, whereas once inside the cave it is virtually out of reach of those agents most responsible for chemical and mechanical weathering, i.e., vegetation and precipitation. Other than frost-splitting of rocky debris occurring near the surface, sediments within the cave are no longer subjected to weathering. As for the effect of water dripping from the roofs of dry caves, Kukla and Lozek (1958) state that water is not

sufficient for chemical disintegration of the filling "because its volume is comparatively small, is relatively saturated with calcium carbonate, and its dissolving ability is very low." Because no soil-forming process takes place in caves, the different developmental phases of soil formed on the surface may be preserved intact. With this in mind, petrographic analysis of the sediments, particularly the clay fraction, was made with the hope that certain minerals or groups of minerals would reflect the nature of

the climate under which they were formed. In this manner, any significant changes in climate in the region could be detected.

Figure 8 is a reproduction of X-ray diffraction patterns of the clay minerals found in the travertine and brown clay units. The travertine unit (2) shows a well-pronounced kaolinite peak and a somewhat depressed peak of mixed layer montmorillonite. The brown clay unit (1) shows a lesser development of kaolinite and a correspondingly higher development of mixed layer montmorillonite. The presence of significant quantities of kaolinite indicates more intense weathering at the time of its formation and reflects a more acidic environment.

Climatic Effects on Clay Mineralogy: Grim (1953) say that

... the temperature and rainfall, particularly its seasonal distribution, are the most significant climate factors. Decay of the parent minerals is most rapid in warm, humid climates. The direction of the movement of water through the weathering zone and the leaching of soluble salts from the material depend on the amount of rainfall and its seasonal distribution. Thus, in a continuously wet climate the movement of the water is downward, tending to move downward the components liberated by the decay of the parent minerals. In a continuously dry climate or one with long dry seasons, the prevailing water movement may be upward, and the decay components would not be

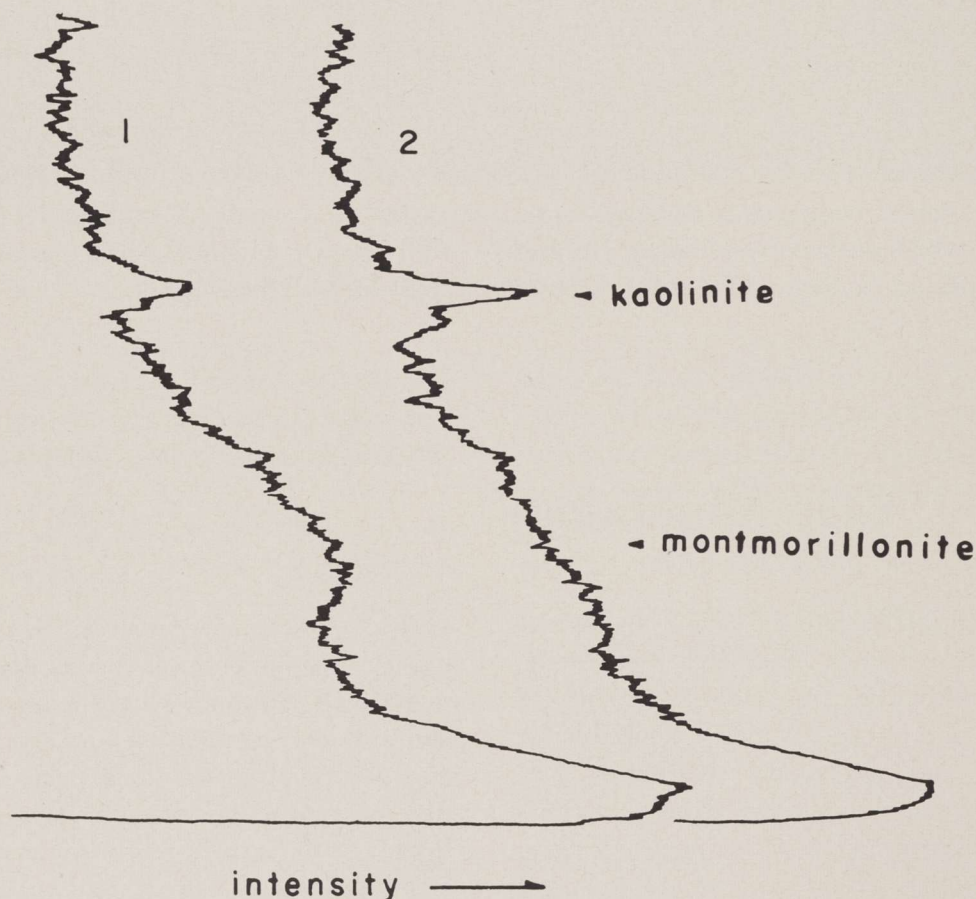


Fig. 8. X-ray diffraction patterns illustrating change in relative intensity for kaolinite and mixed layer montmorillonite. 1) Brown clay unit. 2) Travertine unit.

removed from the decay zone. The climate determines the amount and kind of vegetation and further the amount and kind of organic alteration products yielded by the decay of the organic material. Thus, in a humid cool climate an abundance of organic material decays slowly to produce an abundance of active organic acids and other compounds to react with the parent material, whereas in a hot humid climate with seasonal rainfall the organic material is rapidly destroyed by oxidation and alteration. As a consequence, the kind and amount of organic products available for leaching are very different in the two environments.

The presence of greater amounts of kaolinite in the travertine unit points to an original soil of podsollic or sub-podsolic character, perhaps even a prairie soil. Grim (1953, p. 338) states that such soils

... are developed under cool and damp climatic conditions providing an abundant surface accumulation of organic material. Forests are the most common vegetative cover, although podsolization does occur with grass cover. The covering vegetation must be such as to yield on decomposition organic acids and other compounds of great potency, and there must be enough rainfall to provide active leaching conditions.

The decrease in kaolinite found in the sediments of the brown clay unit indicate a decrease in the intensity of surface weathering, reflecting a shift from the cool and damp climatic conditions during podsolization and travertine formation towards a generally drier situation existing today.

Miller's Cave Local Fauna

The Miller's Cave local fauna was named after Miller's Cave, Llano County, Texas. The animals composing this fauna were recovered primarily from the travertine unit occurring in the south chamber. A large pit was dug in the north chamber, but because of the uncompromising nature of the sediments and the lamentable paucity of bones, further excavation was discontinued and attention was focused on those fossils recovered from the south chamber. For similar reasons, extensive excavation in the south chamber was restricted to the uppermost two beds. The fauna yielded by the sediments below the travertine was considered too sparse to supply any meaningful ecological data. The fauna recovered from the brown clay unit differs from that of the underlying travertine only in that it reflects the beginning of a discernible shift in climatic conditions.

Vertebrata

CLASS OSTEICHTHYES

Fish remains were found only in small numbers. They have not as yet been identified.

CLASS AMPHIBIA

Remains of frogs and salamanders in the travertine unit were not uncommon. Specimens consist primarily of limb bones and vertebrae, although several jaw fragments were recovered. Only *Rana catesbeiana* was identified with any confidence. Several small limb fragments and vertebrae of frogs and salamanders were recovered from the brown clay unit.

CLASS REPTILIA

Snake vertebrae composed the largest single group of non-mammalian skeletal elements in

the travertine. Although several snake mandibles were recovered, most mandibular fragments were lacertilian. Because of their incomplete nature, turtle remains were found to be unidentifiable. Three lizards, *Cnemidophorus* sp., *Sceloporus* sp. and *Crotaphytus* sp., and seven snakes, *Thamnophis sauritus*, *Lampropeltis calligaster*, *Crotalus* sp., *Masticophis* sp., *Opheodrys* sp., *Elaphe* or *Pituophis* sp., and *Tantilla* sp. were recognized. Numerous snake vertebrae were collected from the brown clay along with two incomplete lizard jaws and several pieces of indeterminable turtle shell.

CLASS AVES

The writer was unable to identify any of the fossil birds recovered from the travertine unit, except to determine that most belonged to the Order Passeriformes. Only two unidentifiable tibiotarsal fragments were found in the brown clay.

CLASS MAMMALIA

Systematic Description of the Fossil Mammalia

The systematic section of this paper is intended to supply not only taxonomic information used in the identification of animals in the Miller's Cave local fauna but zoogeographic and ecologic data concerning the described forms as well. Distributional data was derived from two principal sources: Burt and Grossenheider (1952), and Blair, *et al.* (1957). The classification and nomenclature used for Recent species is based on that of Miller and Kellogg (1955). The abbreviation U.T.B.E.G. refers to the collection of the Bureau of Economic Geology, The University of Texas.

Twenty-one species of mammals were identified from the travertine unit and nine of these were found in the brown clay unit. (Table 1).

TABLE 1
Occurrence of Fossil Mammals in
the Miller's Cave Local Fauna

Species	Travertine Unit	Brown Clay Unit	Species	Travertine Unit	Brown Clay Unit
Insectivora			Rodentia		
<i>Blarina brevicauda</i> (Say)	X		<i>Geomys bursarius</i> (Shaw)	X	X
<i>Cryptotis parva</i> (Say)	X		<i>Perognathus hispidus</i> (Baird)	X	X
<i>Scalopus aquaticus</i> (Linnaeus)	X		<i>Reithrodontomys megalotis</i> (Baird)	X	X
			<i>Peromyscus leucopus</i> (Rafinesque)	X	X
			<i>Peromyscus</i> sp.	X	X
Chiroptera			<i>Neotoma floridana</i> (Say & Ord)	X	X
<i>Myotis velifer</i> (Allen)	X	X	<i>Microtus ochrogaster</i> (Wagner)	X	X
unident. sp.		X	<i>Neotoma floridana</i> (Say & Ord)	X	
<i>Eptesicus fuscus</i> (Beauvois)	X		<i>Synaptomys cooperi</i> (Baird)	X	
			<i>Ondatra zibethicus</i> (Linnaeus)	X	
Edentata			Carnivora		
<i>Dasypus bellus</i> (Simpson)	X		<i>Canis</i> sp.	X	
<i>Dasypus novemcinctus</i> (Linnaeus)		X	<i>Ursus americanus</i> (Pallas)	X	
			<i>Mephitis mephitis</i> (Schrober)	X	
Lagomorpha			<i>Spilogale putorius</i> (Linnaeus)	X	
<i>Lepus californicus</i> (Gray)	X		Artiodactyla		
<i>Sylvilagus</i> sp.	X	X	<i>Odocoileus</i> sp.	X	

Class MAMMALIA

Order INSECTIVORA

Family Soricidae

Genus *Blarina* Gray, 1838

Blarina brevicauda (Say), 1823

Fig. 10 C&D

Geologic Range—Pleistocene (Kansan?) to Recent.

Distribution—Forests and grasslands of eastern half of the United States and adjacent Canada west to a line from Corpus Christi, Texas to north central North Dakota (Fig. 8).

Habitat—The short-tailed shrew is commonest in eastern United States and southeastern Canada where it is found in deciduous or coniferous forests and in open fields. In the Great Plains it is limited to westward extensions of the deciduous forests along watercourses or to lush grassy areas near water (Hall and Kelson, 1959).

Remarks—This shrew is represented by thirteen whole or fragmentary mandibles, most with partial dentitions (U.T.B.E.G. 40540-19, 20). Anteroposterior length of the only two complete lower jaws from the dorsal articular facet of the condyle to the tip of the incisor was 13.8 mm. and 13.2 mm. These fall within the size range of *B. brevicauda carolinensis* now living in Kansas and Oklahoma. In the fossil specimens the postero-internal ramal fossa of the dentary is very deep and broad and is almost rectangular in outline. Immediately above this fossa lies a shallow but distinct fossette, and ventral to the fossa occur two small foramina. The mental foramen just below M_1 is surrounded by a distinct depression which broadens anteriorly. On the lingual surface of the ascending ramus and originating from the coronoid process is the slender spicular process which extends in a posterolateral direction (Fig. 6). These characters as well as those of the dentition agree

closely with those of Recent *B. brevicauda* as described by Gaughran (1954).

Genus *Cryptotis* Pomel, 1948

Cryptotis parva (Say), 1823

Geologic Range—Pleistocene (Illinoian) to Recent.

Distribution—Grassy habitats in eastern United States south of a line from central New York to northeastern Iowa and northwestern Kansas and west through Kansas, Oklahoma, and all but trans-Pecos Texas.

Habitat—The least shrew is found in grassy meadows and woody situations, but seems to prefer open grasslands.

Remarks—The four fossil mandibles (U.T.-B.E.G. 40540-21) are identical in size and condition of teeth and jaws with Recent *C. parva*.

Family Talpidae

Genus *Scalopus* E. Geoffrey St.-Hilaire, 1803

Scalopus aquaticus (Linnaeus), 1758

Geologic Range—Late Pleistocene (Wisconsin) to Recent.

Distribution—Eastern United States south of a line from western Nebraska to south central Texas.

Habitat—Sandy, or moist loamy soils rich in organic matter. Feeds mostly on earthworms, grubs, and insects.

Remarks—Remains of the eastern mole include portions of seven lower jaws (U.T.B.-E.G. 40540-23), four of which possess partial dentitions.

Order CHIROPTERA

Family Vespertilionidae

Genus *Myotis* Kaup, 1829

Myotis velifer (Allen), 1890

Geologic Range—Late Pleistocene (Wisconsin) to Recent.

Distribution—From Guatemala and Mexico north into the United States from western Arizona to central Texas and north to northeastern Utah and western Nebraska.

Habitat—Colonial and usually a cave dweller, although it has been found in fissures in limestone rocks.

Remarks—The little cave bat occurs in Miller's Cave today in vast numbers. It is also one of the most commonly preserved fossil forms. Specimens include numerous lower jaws (U.T.B.E.G. 40540-24), two maxillary fragments (40540-25), and scores of complete and fragmented long bones (40540-26).

Genus *Eptesicus* Rafinesque, 1820

Eptesicus fuscus (Beauvois), 1796

Geologic Range—Late Pleistocene (Wisconsin) to Recent.

Distribution—From Central America throughout Mexico and the United States and into Canada.

Habitat—Normally a forest dweller, but utilizes crevices in caves and rocks as daytime retreats. Favorite roosts are under the loose bark of dead trees and in cavities of trees (Davis, 1960).

Remarks—Known specimens include 16 lower jaws (U.T.B.E.G. 40540-27) and one large maxillary with partial dentition (40540-28). Except for its much larger size, the big brown bat closely resembles *Myotis velifer*. Common in the cave sediments, no live individuals of this species were observed during the year excavation was carried out.

Order EDENTATA

Family Dasypodidae

Genus *Dasypus* Linnaeus, 1758

Dasypus bellus Simpson, 1929

Geologic Range—Late Pleistocene (Sangamon to Wisconsin).

Distribution—Fossil specimens are known

from localities in Florida, Texas, Oklahoma, and Missouri.

Habitat—Prefers shrubby or woody areas with moist, friable soil, especially where there is a floor of rapidly decaying vegetation.

Remarks—This large armadillo is represented by portions of five movable ring scutes, three buckler scutes, and one leg scute (U.T.B.E.G. 40540-30). These scutes are approximately the same size as the ones described by Simpson (1929) from Florida, and by Slaughter (1959) from Texas. Slaughter (1961) discusses the significance of *D. bellus* in Pleistocene local faunas by noting the ecological requirements of its smaller counterpart, *D. novemcinctus*. As armadillos require vast quantities of insect food (Kalmbach, 1943) it is thought that the absence of sufficient numbers of insects is probably the limiting factor on the distribution of the living armadillo in parts of Mexico and West Texas. Because of its much greater size, *D. bellus* would be subject to even greater limitation by the food factor. Slaughter (1959, p. 312) states that

... by far the majority of insects suitable for armadillos require rapidly rotting wood or deep moist soil. In area where there is little or no soil and the ground is dry or where fallen wood remains dry and decomposes very slowly, insects that lend themselves to the armadillo's foraging technique are not simply less in number, they are essentially not present. Whether or not this is the reason for *D. novemcinctus* avoiding truly arid country, its range expansion has stopped along the eighteen to twenty-inch per annum rainfall belt, through Mexico and in the United States.

The living armadillo is also limited in its distribution by low temperatures. Although it is able to find considerable protection from the cold by remaining in its burrow, severe winters and bad weather in fall and spring have killed many and appear to have halted further advance of the species. It should be mentioned

that the Miller's Cave local fauna marks the minimum terminal date for *D. bellus* (see Age and Correlation, p. —). The youngest reported date prior to this find was 9,550 B. P. in the Ben Franklin local fauna (Slaughter and Hoover, 1963).

Order RODENTIA

Family Geomyidae

Genus *Geomys* Rafinesque, 1817

Geomys bursarius (Shaw), 1800

Geologic Range—Pleistocene (Illinoian) to Recent.

Distribution—Northwestern Minnesota to Gulf of Mexico; east of eastern front of Rocky Mountains; west of Mississippi River except for populations in southern Wisconsin, southern and eastern Iowa, and northwestern Illinois.

Habitat—Found generally where there is a deep, primarily sandy soil favorable to burrowing. Feeds mostly on roots and tubers, but also eats grubs, beetle pupae, and crickets.

Remarks—Remains of the plains pocket gopher consist of five mandibles with partial tooth rows (U.T.B.E.G. 40540–40), many toothless mandibles (40540–41), and numerous incisors (40540–42). Characters of the fossil specimens are indistinguishable from those *Geomys bursarius* living in Texas today,

Family Heteromyidae

Genus *Perognathus* Wied-Neuwied, 1839

Perognathus hispidus Baird, 1858

Geologic Range—Late Pleistocene (Sangamon) to Recent.

Distribution—Entering United States from Mexico from southern Texas to southeastern Arizona; ranging northward between eastern front of Rocky Mountains and eastern forest, through Nebraska and South Dakota (west of Missouri River).

Habitat—Prefers open areas, especially grasslands; found in both tall grass and short grass prairies.

Remarks—The plains or hispid pocket mouse is represented by a relatively complete palate with both tooth rows possessing P^1-M^2 (U.T. B. E. G. 40540–44), a left maxillary with P^1-M^1 (40540–45), and a left mandible with P_4-M_2 (40540–46). These correspond closely in size and dentition to Recent specimens of *P. hispidus*.

Family Cricetidae

Genus *Neotoma* Say and Ord, 1825

Neotoma floridana Say and Ord, 1825

Fig. 11, C & D.

Geologic Range—Pleistocene (Illinoian) to Recent.

Distribution—Southern Florida to southeastern North Carolina and west on Coastal Plain to Edwards Plateau in Texas; north in Mississippi embayment to southern Indiana; also north through Arkansas, Oklahoma, Kansas, and Nebraska to southwestern South Dakota (Fig. 8).

Habitat—Usually inhabits wooded or brushy lands, but can be found in swamplands, forested uplands, and grassy plains.

Remarks—Remains of the wood rat are among the most numerous recovered from the cave sediments. Most of these remains are in the form of isolated molars (U.T.B.E.G. 40540–27), but dentaries with associated teeth (40540–48) are fairly common. Only one definitely assignable maxillary fragment (40540–49) was recovered. Because of the extremely similar specific characters and the high level of individual variation within the genus *Neotoma*, it was found to be exceedingly difficult to separate these specimens according to species. Variations in enamel patterns with different stages of wear also led to considerable

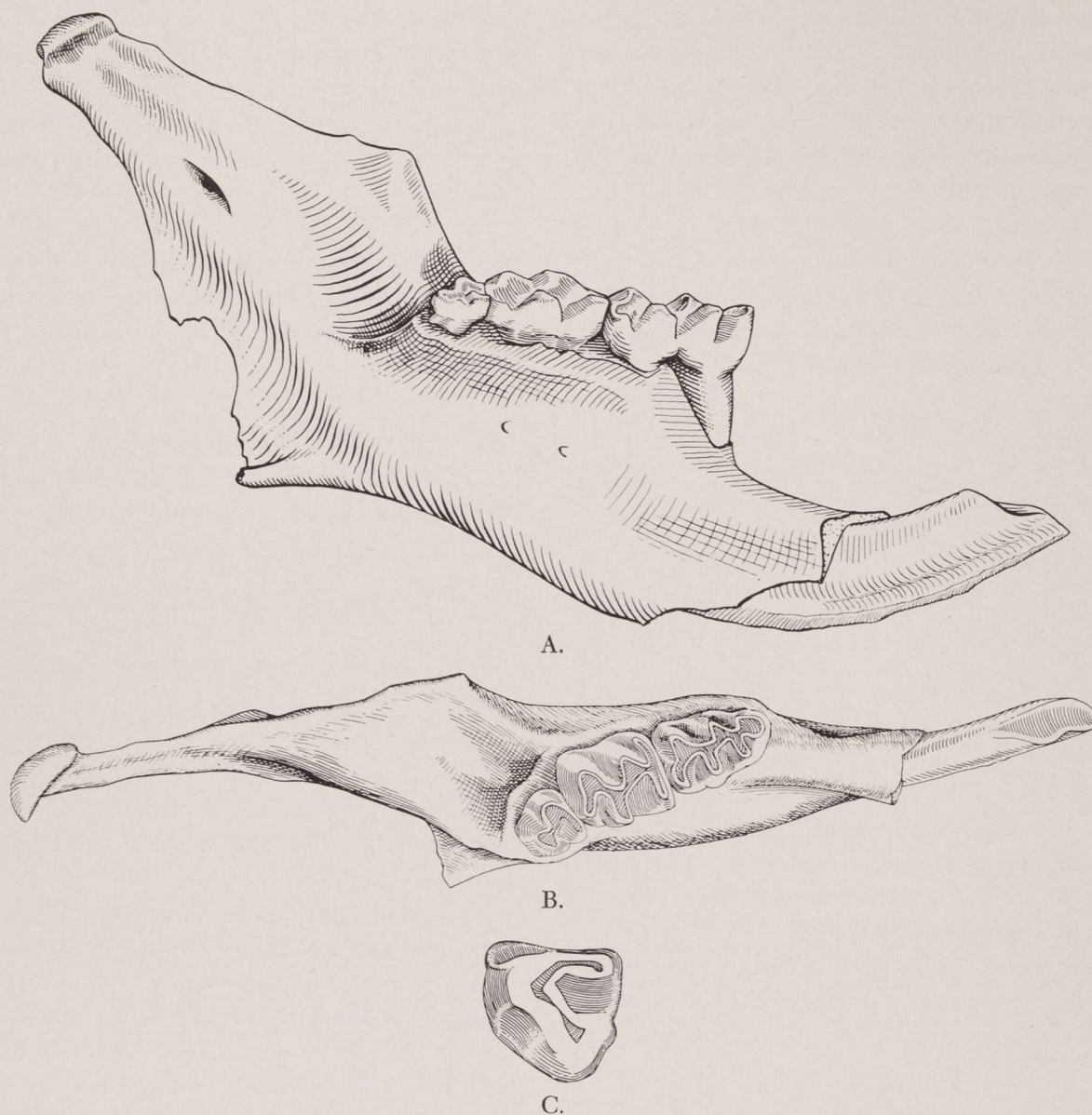


Fig. 9. Ramus and (lower) M_3 of *Reithrodontomys megalotis* (U.T.B.E.G. 40540-11). A. Labial view of right ramus. B. Occlusal view of right ramus. C. Occlusal view of right M_3 .

confusion. Hibbard and Taylor (1960), however, have suggested one possible means of separating *N. floridana* and *N. micropus*. The anterior loop of M^1 of both species is divided into two confluent alternating triangles; the anterior or labial (external) and the posterior

or lingual (internal). The side of the posterior or lingual alternating triangle is flattened in *N. floridana*; in *N. micropus* this triangle is rounded. The anterior loop of the M^1 in the fossil specimens agrees with *N. floridana* in this respect. (Fig. 11, C & D).

Genus *Reithrodontomys* Giglioli, 1874
Reithrodontomys megalotis Baird, 1858
Fig. 9, A, B, C.

Geologic Range—Late Pleistocene (Sangamon) to Recent.

Distribution—From southwestern Canada south through western United States into southern Mexico; in the north, ranging east into southern Wisconsin and in the south, east into trans-Pecos Texas.

Habitat—Found predominantly in open situations; generally most abundant in rather dense growths of grass, forbs, and other low-lying vegetation near water, as in meadows, marshes, and stream valleys (Hooper, 1952).

Remarks—Remains of the western harvest mouse are relatively abundant in this deposit. Forty-four lower jaws lacking teeth (U.T.-B.E.G. 40540-10) and two lower jaws with complete tooth rows were recovered (40540-11). This species was separated from *R. humulis* and *R. fulvescens* on characters of the M_3 . The major fold of M_3 is developed but remains quite shallow. The first primary fold of M_3 is broad and reaches halfway across the tooth, while the hypoconid lies on the lingual side of the tooth, posterior to the metaconid. These characters are identical with those of Recent specimens of *R. megalotis*. Length of mandibular tooth rows of the two complete jaws is 3.1 mm. and 2.9 mm.

Genus *Peromyscus* Gloger, 1841
Peromyscus leucopus (Rafinesque), 1818

Geologic Range—Late Pleistocene (Wisconsin?) to Recent.

Distribution—Eastern United States north of a line from southwestern Mississippi to northeastern North Carolina; west to western Montana and eastern Arizona; south through eastern Mexico to Yucatan.

Habitat—Primarily woodlands; along the

western limits of its range, it is restricted almost entirely to river and creek bottoms; it is almost never found in prairie lands. Davis (1960) states that white-footed mice are good climbers and often make their dens in hollow trees out of danger of flood waters. They also utilize logs, stumps, and brush piles.

Remarks—The seven mandibular specimens (U.T.B.E.G. 40540-12) of *P. leucopus* recovered are distinctly larger than Recent specimens of either *P. maniculatus* or *P. pectoralis*. Anteroposterior length of M_1 - M_3 is 3.3 mm., and the length of the only complete lower jaw (from the posterior border of the coronoid process to the anterointernal end of dentary) is 8.1 mm.

Peromyscus sp.

Remarks—Scores of toothless mandibles (U.T.B.E.G. 40540-13) of the genus *Peromyscus* were recovered from the travertine unit. They are considerably smaller than those jaws assigned to *P. leucopus*, but because of the lack of preserved dentitions, specific identification was not made.

Subfamily Microtinae
Genus *Synaptomys* Baird, 1858
Synaptomys cooperi Baird, 1858
Fig. 10, A, B.

Geologic Range—Late Pleistocene (Sangamon) to Recent.

Distribution—From southeastern Canada west to western Minnesota, south to southwestern Kansas, northeastern Arkansas, southeastern Tennessee, and northeastern North Carolina (Fig. 12).

Habitat—Usually found in moist situations. Howell (1927) states that *S. cooperi* is of definite boreal affinity and although it has been trapped in moist and dry grass lands, in the warmer parts of its range it is confined for the most part to cold sphagnum bogs.

Remarks—The southern bog lemming is represented by dentary fragments (U.T.B.E.G. 40540-5, 6), several mandibles with partial dentitions (40540-1, 2, 3, 4) and several individual molars (40540-7). Fossil specimens agree closely in size and dentition with specimens of Recent *S. cooperi*. They are distinctly smaller than specimens described as *S. australis* by Simpson (1928). Anteroposterior length of M_1 - M_3 of the only complete dentition (40540-1) is 7.4 mm.

Hibbard (1963, in press) has noted a north-south cline in two characters of *S. cooperi*. One is a size cline and is characterized by a progressive increase in size of the subspecies of *S. cooperi* from north to south. The largest *Synaptomys* known, *S. australis*, is found in far southern fossil localities and may represent a continuation of this series. The specimens of *S. cooperi* from Miller's Cave are of intermediate size and fall into the size range of *S. cooperi paludis* (Hibbard and Rinker, 1942), living in southwest Kansas today. The second cline is concerned with the posterior extension of the lower incisor to and beyond the M_3 . It appears that in the more northern parts of its distribution the lower incisor of *S. cooperi* reaches the middle of M_3 , while in the more southern forms the incisor extends well past the M_3 (Fig. 12). Intermediate forms are characterized by intermediate conditions of this feature. The incisor of *S. cooperi* from Miller's Cave extends beyond M_3 , but not so far as that in *S. australis*.

Genus *Microtus* Schrank, 1798

Microtus ochrogaster (Wagner), 1842

Fig. 11, B.

Geologic Range—Pleistocene (Illinoian) to Recent.

Distribution—From central Oklahoma into southern Canada; west to central Colorado and

Wyoming and southeastern Montana; east into Ohio and western West Virginia (Fig. 7).

Habitat—Mostly inhabits tall-grass prairies, living in colonies and utilizing underground burrows and surface runways under lodged vegetation for concealment and protection (Davis, 1960).

Remarks—The prairie vole is among the most abundantly represented rodents in this fauna. Specimens consist of two partial skulls with all but the third molars present (U.T.B.E.G. 40540-50), two maxillary fragments with associated M^1 and M^2 (40540-51), at least fifty mandibular elements, most with associated molars (40540-52), and scores of individual molars (40540-53).

Separation of several of the living species of the genus *Microtus* on the basis of skeletal material is extremely difficult, if at all possible. This is especially true of *M. ludovicianus*, *M. ochrogaster* and *Pitymys pinetorum*. These are assigned by some authors to two species groups, *Pedomys* and *Pitymys*, which Bailey (1900) considered to be subgenera of the genus *Microtus*. Subsequent workers classified *Pitymys* as a separate genus, and more recently Hibbard (1958) and Davis (1960) elevated *Pedomys* to the same rank. Still others, particularly Hall and Cockrum (1953) and Hall and Kelson (1959, p. 750), use Bailey's original classification "... because of our inability to distinguish the skulls of some specimens of *Microtus ochrogaster* in eastern Kansas from those of *Microtus pinetorum* in the same area."

Microtus ludovicianus and *M. ochrogaster*, members of the *Pedomys* group, are believed by some to be allopatric members of the same species (Davis, 1960, Bailey, 1905). There appears to be no way to separate the two species. Enamel patterns of *M. ochrogaster* and *P. pinetorum* are practically identical except for one character. The second re-entrant angle on

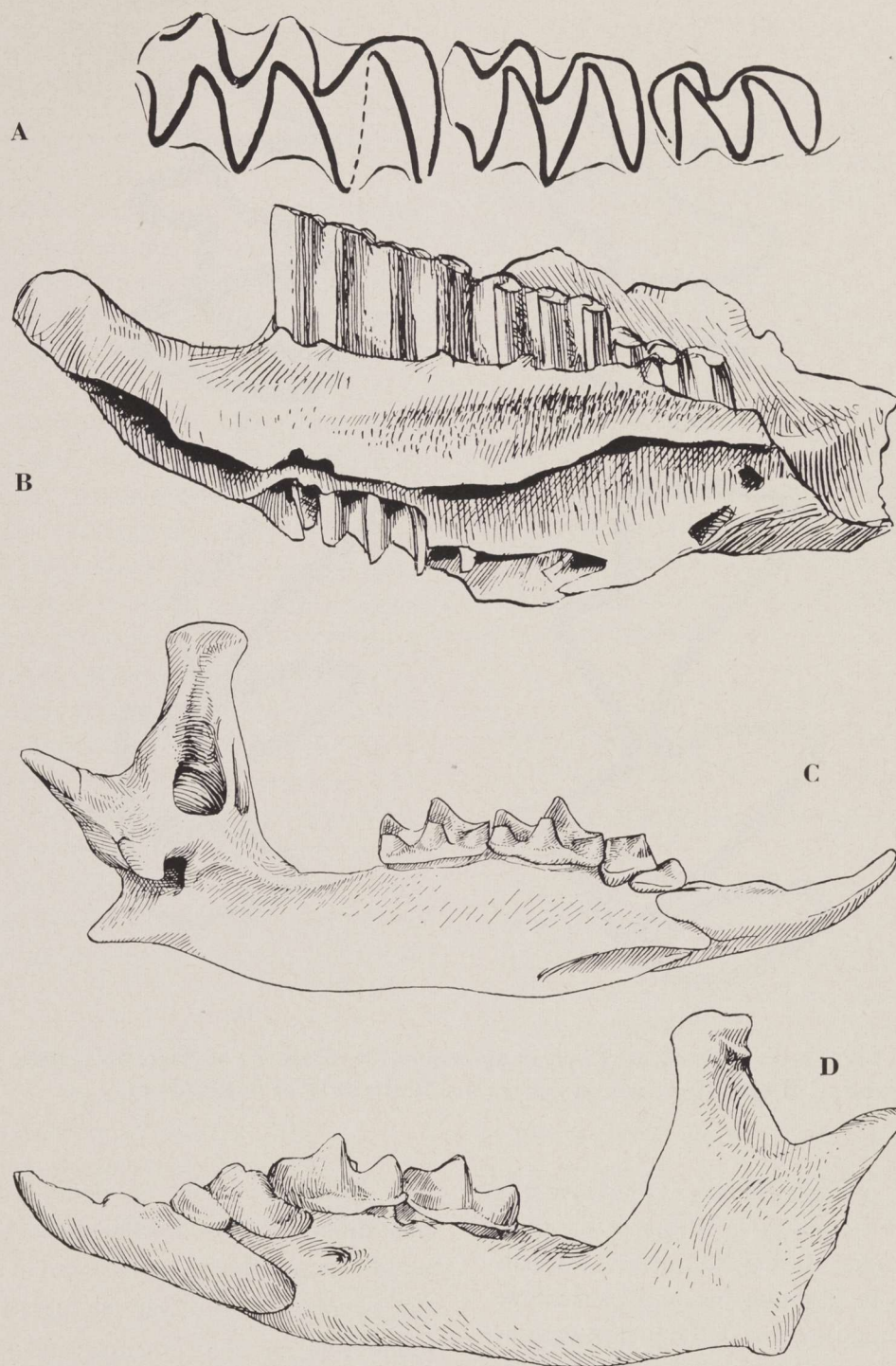


Fig. 10. A, B, C, D. Ramus and dentition pattern of *Synaptomys cooperi* (U.T.B.E.G. 40540-1) and rami of *Blarina brevicauda* (40540-20). A. Enamel pattern of right $M_1 - M_3$ of *Synaptomys cooperi*. B. Lingual view of right ramus of *S. cooperi* x 5.75. C. Lingual view of left ramus of *Blarina brevicauda* x 10. D. Labial view of left ramus of *B. brevicauda* x 11.2.

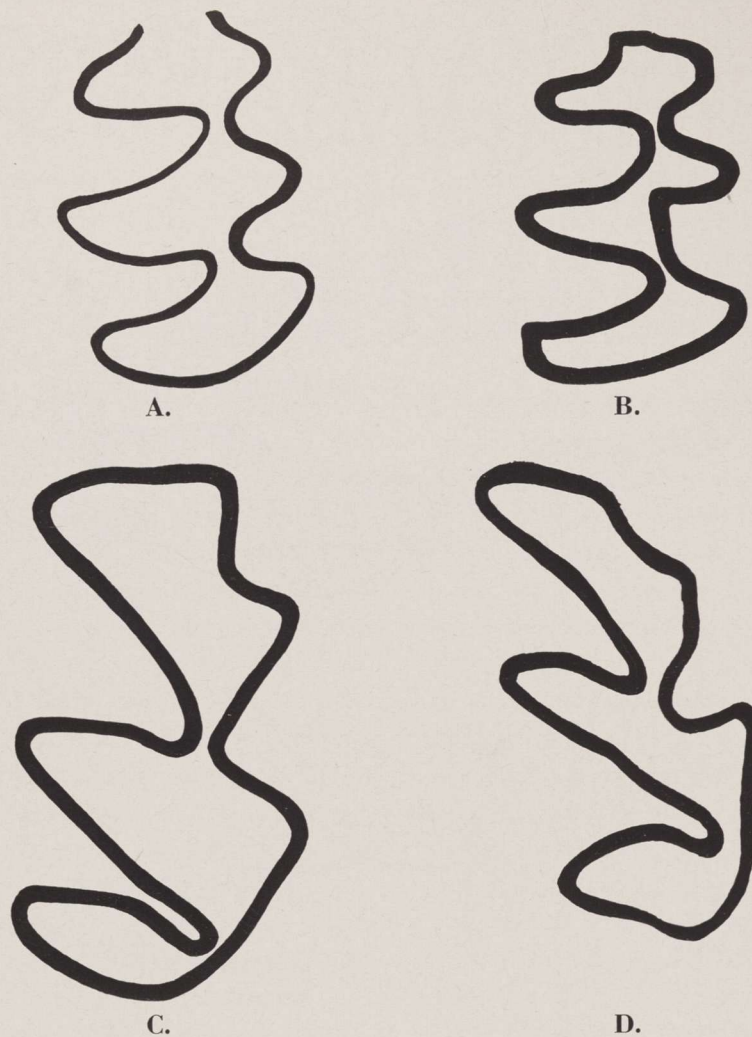


Fig. 11. A. Right M_3 of *Pitymys pinetorum*. B. Right M_3 of *Microtus ochrogaster*. C. Right M^1 of *Neotoma micropus*. D. Right M^1 of *N. floridana*.

the M_3 of *M. ochrogaster* may extend medially and abut on the posterior border of the third re-entrant angle, closing the second alternating triangle. In *Pitymys* this angle is shallow; its apex lies opposite that of the first re-entrant angle medially, and the second alternating triangle always remains open (Fig. 11 A, B). Accordingly, an M_3 with a constricted or divided middle loop may be assigned to *M. ochrogaster*, but one lacking this constriction

may belong to either *M. ochrogaster* or *P. pinetorum*. The constricted condition of the middle loop of the M_3 was present in sixteen of the twenty-five available comparative specimens of Recent *M. ochrogaster* and was absent in the six available specimens of *P. pinetorum*. Of the many individual *Microtus* molars recovered, only two were identified as M_3 . Both of these had a constricted middle loop.

Genus *Ondatra* Link, 1795

Ondatra zibethicus (Linnaeus), 1766

Geologic Range—Pleistocene (Illinoian) to Recent.

Distribution—Throughout most of North America north of Mexico, except Florida and a coastal strip in Georgia and South Carolina. Also most of Texas (excluding Panhandle, trans-Pecos, and extreme southeast) and most of California.

Habitat—Inhabitant of streams or lake shores or marshes. Hollister (1911) states that the muskrat is a builder of marsh houses and spends most its time in the water.

Remarks—Remains of the common muskrat are quite common in the travertine unit. Specimens consist primarily of mandibles with at least partial dentitions (U.T.B.E.G. 40540–40), although several maxillary fragments (40540–56) have been recovered. All elements compare closely with Recent specimens of *O. zibethicus*. Measurements on the only nearly complete jaw are as follows: length of M_1 – M_2 is 8.9 mm., diastemal length is 9.4 mm., breadth of mandible is 6.9 mm. Lengths of M_1 in four specimens are (in mm.) 5.8, 6.4, 6.0, and 6.5.

Order CARNIVORA

Family Ursidae

Genus *Ursus* Linnaeus, 1780

Ursus americanus Pallas, 1780

Geologic Range—Late Pleistocene (Wisconsin?) to Recent.

Distribution—From Alaska across Canada; once ranged throughout most of the United States; now extirpated in many parts of its former range.

Habitat—Mostly woodlands and forested areas.

Remarks—The black bear is represented by a right M_1 (U.T.B.E.G. 40540–60) and by the

first and second phalanges of the right front foot (40540–61). Length of RM_1 is 22.5 mm. and width is 14.1 mm. Although this molar is larger than all of the *U. americanus* specimens available for comparison, it is distinctly smaller than that of *U. horribilis*.

Family Canidae

Genus *Canis* Linnaeus, 1758

Canis sp.

Remarks—This genus is represented by a single LM^2 (U.T.B.E.G. 40540–65). Total length of this tooth is 12.5 mm. Width trigonid is 7.9 mm. and width talonid is 6.4 mm. It is larger than the LM^2 of the coyotes compared to it, and slightly larger than the one specimen of *C. niger* available.

Family Mustelidae

Genus *Mephitis* St.-Hilaire and Cuvier, 1795

Mephitis mephitis (Schreber), 1776

Geologic Range—Late Pleistocene (Wisconsin) to Recent.

Distribution—From Mexico throughout the United States and into Canada.

Habitat—Inhabitant of wooded or brushy areas; rocky outcrops favorite sites of refuge, but also utilizes burrows of armadillos, foxes and other animals (Davis, 1960).

Remarks—The striped skunk is represented by three teeth: an M^1 (U.T.B.E.G. 40540–69), a P^1 (40540–70), and an M_1 (40540–71). These teeth compare in every respect with those of the Recent species.

Genus *Spilogale* Gray, 1865

Spilogale putorius (Linnaeus), 1758

Geologic Range—Late Pleistocene (Wisconsin) to Recent.

Distribution—Eastern United States from peninsular Florida north to Ohio River and southern Pennsylvania, and, west of Mississip-

pi River, north to northern Minnesota and northern South Dakota; west to central Texas, eastern Colorado, and southeastern Wyoming.

Habitat—Occurs in wooded areas mainly and tall-grass prairies, preferring rock canyons and outcrops (Davis, 1960).

Remarks—Numerous teeth (U. T. B. E. G. 40540-72) and mandibular fragments (40540-73) of this species were collected. It is separated from *Mephitis* by its smaller size and on characters of the M₁, especially the trigonid.

Order LAGOMORPHA

Family Leporidae

Genus *Lepus* Linnaeus, 1758

Lepus californicus Gray, 1837

Geologic Range—Late Pleistocene (Yar-mouth) to Recent.

Distribution—From southern South Dakota, eastern Nebraska, western Missouri, and Arkansas and eastern Texas to the Pacific Coast and north to southern Washington; south into Mexico.

Habitat—Open grasslands with scattered stands of herbaceous vegetation.

Remarks—Remains of the black-tail jackrabbit are extremely rare in this deposit. Specimens, including several isolated molars and a manibular fragment (U.T.B.E.G. 40540-31), were identified primarily by their conspicuously large size.

Genus *Sylvilagus* Gray, 1867

Remarks—Rabbit remains are abundantly represented, consisting of numerous mandibular fragments with partial dentitions (U.T.B.-E.G. 40540-32), isolated molars (40540-33), and several skull elements (40540-34). The writer was unable to make any specific identifications.

Order ARTIODACTYLA

Family Cervidae

Genus *Odocoileus* Rafinesque, 1832

Remarks—Identification of this genus is based on the presence of a single lower molar (U.T.B.E.G. 40540-75). The writer was unable to distinguish between *O. virginianus* and *O. hemionus* because of the obscured cusp pattern on the lone specimen.

Paleoecology and Zoogeography

Figures 12 and 13 indicate the present geographic distribution of some of the less ecologically tolerant members of the Miller's Cave local fauna. It is readily noted that there has been a distinct shift in distribution of these species. *Synaptomys cooperi* and *Microtus ochrogaster* have shifted their distributions far

to the north of the Llano region while such species as *Blarina brevicauda*, *Neotoma floridana*, and *Ondatra zibethicus* are now primarily eastern (Austro-riparian) forms. What factors account for these patterns?

All of the basic habitat requirements govern the distribution of animals, but the critical fac-

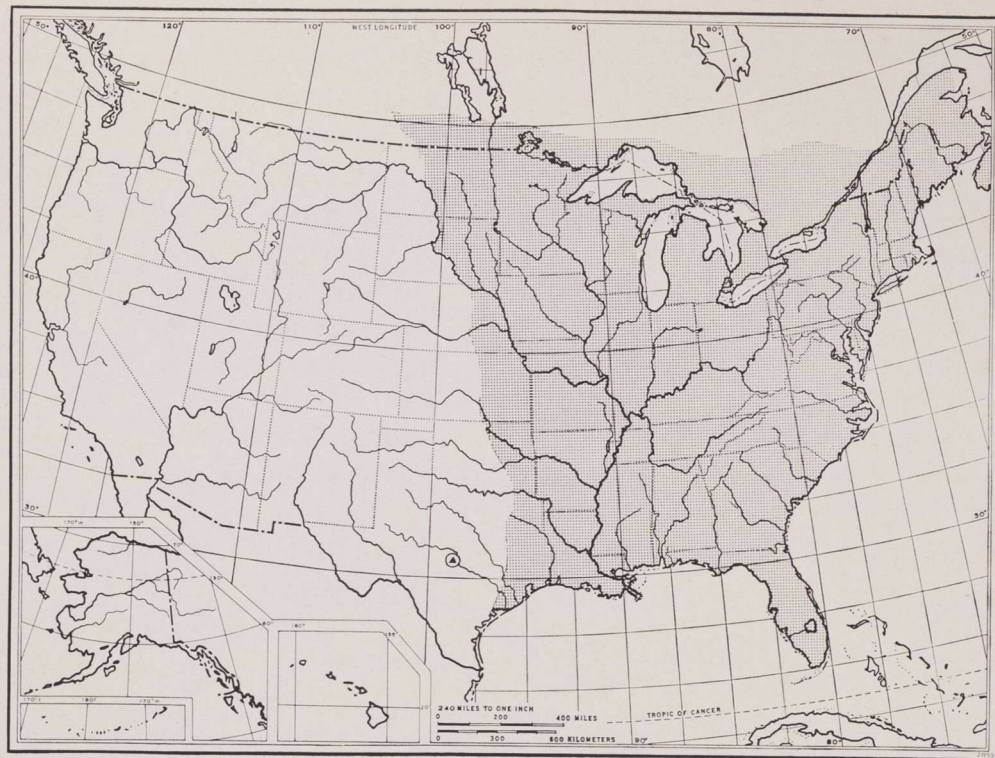
Fig. 12. Distribution maps of Recent *Synaptomys cooperi* and *Microtus ochrogaster*. Shaded parts of the maps represent the areas within which each species might be expected, given suitable conditions. The black triangles represent the approximate location of Miller's Cave.



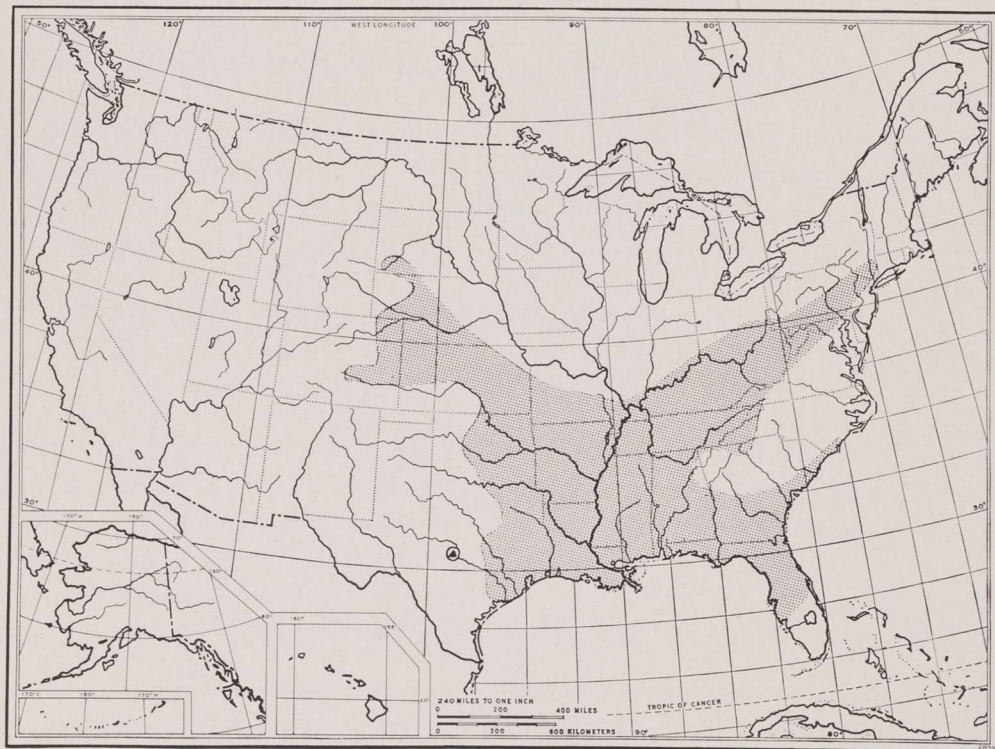
SYNAPTOMYS COOPERI



MICROTUS OCHROGASTER



BLARINA BREVICAUDA



NEOTOMA FLORIDANA

Fig. 13. Distribution maps of Recent *Blarina brevicauda* and *Neotoma floridana*.

tors are those which are most subject to variation. Temperature, humidity, and food and water supply vary to a great degree, and these factors accordingly are the most important causes in variation in animal distribution. Liebig's "Law of the Minimum" (Allee, *et al.*, 1949, p. 198), which states roughly that in plants the food element which is least abundant in proportion to the plant's needs limits its existence, may be extended to cover the effect of the environment upon animals since that factor for which a species has the narrowest range of tolerance limits its existence. As mentioned, one of the limiting factors responsible for the patterns of distribution outlined immediately above is temperature. Merriam (1899) postulated that

... the northward distribution of terrestrial animals and plants is governed by the sum of the positive temperatures for the entire season of growth, and southward distribution is governed by the mean temperature of a brief period during the hottest part of the year.

The quantity and seasonal distribution of rainfall also plays a critical role. The amount of humidity is an important limiting factor not only with respect to the physiological requirements of individual species, but also in that it controls the physical nature of the habitat and the type and quantity of food available. A deficiency in rainfall precludes the existence of such hygric environments as permanent streams, lakes, swamps, and bogs. It also reduces the amount of vegetation available for food and cover, in turn affecting soil development and runoff. Thus, a change in the amount of either one of the two above mentioned factors could result in the withdrawal of certain species from their former range.

In order to reconstruct the climatic and environmental conditions prevailing at the time the Miller's Cave local fauna lived, the ecology of the individual members of the fauna should

be critically examined. It is assumed that the fossil forms had the same habitat preferences and were subject to the same physiological and ecological limitations as the living members of their species group. Further, it is believed that forms which have the narrowest ecological tolerances provide a more accurate basis for reconstruction of paleoecology. Some of these forms are as follows:

Synaptomys cooperi—usually found in moist situations. Howell (1927) states that *S. cooperi* is of definite boreal affinity and although it has been trapped in moist and dry grass lands, in the warmer parts of its range it is confined for the most part to cold sphagnum bogs.

Ondatra zibethicus—inhabitant of streams or lake shores or marshes, especially where there are heavy growths of rushes and cattails. A builder of marsh houses, it spends most of its time in the water.

Scalopus aquaticus—occurs largely in moist, sandy soils rich in organic matter. Feeds mostly on earthworms, grubs, and insects.

Blarina brevicauda—prefers soft, damp soil in wooded areas and their associated meadows and openings, especially where there is a floor of decaying organic matter. Restricted to eastern United States, but ranges westward along moist stream valleys which support moderate amounts of trees and shrubs.

Reithrodontomys megalotis—found predominantly in open situations; generally most abundant in rather dense growths of grass, forbs, and other low-lying vegetation, as in meadows, marshes, and stream valleys.

The above species simply could not survive and flourish under the conditions prevailing in the Llano area today (CLIMATE, p. 7). Insufficient annual rainfall and long periods of drought prohibit the development of such rela-

tively permanent bodies of water as marshes and bogs, and although there is a well-developed drainage system in the region, many of the smaller streams are dry during certain parts of the year. Growth of the more water-dependent vegetation is prevented, accumulation of deep soils, and spread of extensive grasslands and meadows are effectively inhibited, with the consequent loss of their respective ecologic niches. Temperatures undergo wide variation, with summer highs reaching as much as 115° F. Many forms are unable to withstand such temperatures. *Microtus ochrogaster* was found to be unable to tolerate temperatures greater than 98° F. (Dice, 1922). Although differences in temperature of micro-environments may compensate for this to some degree, such an animal would hardly be expected to flourish in an environment where critically high temperatures are common for long periods of time.

Ecologic tolerances and habitat preferences of these species indicate that the climate of the Llano region was much more moist than it is today. Rainfall was not only somewhat greater, but probably more evenly distributed throughout the seasons. Because of greater soil development and vegetation cover, runoff was lessened and rainfall was thereby rendered more effective. An increase in cloud cover associated with the more moist climate served to reduce evapotranspiration rates as well as to provide a filter for some of the sun's harmful radiation.

The climate of the Llano region may have been generally cooler, with a distinctly lower mean annual temperature, but a similar effect could have been accomplished by eliminating the extremes, especially the summer one. Thus, instead of a general overall drop in seasonal temperatures, the extreme summer highs of the present could have been non-existent at the time the fauna lived, resulting in a more

equable and a more tolerant environment for most species.

It might be well to emphasize the fact that seasonal temperatures were not necessarily much lower. Much of the work dealing with climate of the Pleistocene during glacial times has been based on the assumption that distribution changes and the like were caused by generally colder conditions, whereas there is much evidence to the contrary (Hibbard, 1960). Many of the conditions necessary for survival of the supposedly more cold-adapted animals can be provided by the presence of sufficient amounts of water. Other species are able to survive solely as a result of slight amelioration of temperature extremes, especially the summer ones in the lower latitudes, but the critical factor appears to be rainfall. The combination of higher rainfall and reduction of seasonal temperature extremes is one which quite satisfactorily explains many of the problems resulting from changes in animal distribution. It certainly does not exclude the possibility of colder climatic conditions, but it should be seriously considered before colder temperatures are automatically assumed.

Finally, fossil forms allow recognition of four different communities which existed in the Miller's Cave region and which contributed elements to the fossil fauna: The stream and marsh border community, the lowland meadow community, the shrub and tree community, and the upland prairie community (after Stephens, 1959). A species assigned to a particular community is not necessarily restricted to that one, but may be simply representative of it.

Stream and Marsh Border Community: Animals belonging to this community are the fishes, some salamanders and some frogs, and the muskrat. All of these forms are closely dependent on, and spend most of their lives in and around water. The western harvest mouse

(*Reithrodontomys megalotis*) could be assigned to such a community, but is generally found in a slightly drier situation. The southern bog lemming is probably equally at home in this as well as in the lowland meadow community.

Lowland Meadow Community: Forms characteristic of this association are the prairie vole, the southern bog lemming, the eastern mole, the little short-tale shrew (*Cryptotis*), the western harvest mouse, and possibly the plains pocket gopher. Their presence suggests the existence of a moist, deep soil, rich in organic matter, and covered with a thick growth of grasses.

Shrub and Tree Community: The recovery of relatively numerous specimens of the short-tail shrew (*Blarina*), the Florida woodrat, the extinct armadillo, and the cottontail rabbit in-

dicate a well-developed association of trees and shrubs. *Blarina* prefers wooded areas with a floor of leaf litter, whereas *Neotoma* and *Dasypus* favor brushy and woody areas for nesting, burrowing, and feeding. The white-footed mouse is adept at climbing and often dens in hollow trees. In places not in danger of flooding, it lives in dens under logs, in stumps and in brush piles. Such forms as the spiny lizard (*Sceloporus*), the passerine birds, the black bear, and the striped skunk (*Mephitis*) also belong to this community.

Upland Prairie Community: The hispid pocket mouse and the black-tailed jackrabbit prefer open grasslands with scattered stands of herbaceous vegetation. The spotted skunk (*Spilogale*) is abundant in both wooded areas and tall grass prairies. The striped skunk may also be at home here.

Age and Correlation

On the basis of information derived from paleoecology and zoogeography, the Miller's Cave Local Fauna is believed to be of Late Wisconsin age. The fossil mammals found in the deposit differ from their respective living species only in that the distributions of several of the members have shifted. The southward and westward expansion of the ranges of forms which require cooler and more moist conditions for survival is correlated with the southward extension of the continental ice sheet during Wisconsin time. A radiocarbon date of $3,008 \pm 410$ B.P. years (Socony-Mobil, SM-596) was obtained from a charcoal sample at the base of the brown clay unit. An age of $7,200 \pm 300$ years B.P. (Radiocarbon Dating

Laboratory, The University of Texas, A-326) was obtained for a sample of bone from the travertine unit. The fauna compares well with other known glacial faunas (Hibbard, 1958) and also indicates a Wisconsin age for the travertine-cemented deposit. Only one species, *Dasypus bellus*, is extinct, and it has been recovered from known Wisconsin faunas. Furthermore, there appears to be an uninterrupted sequence of events leading gradually from the more moist, perhaps cooler, conditions during travertine formation to the hotter, semiarid conditions of the present. There is no evidence for a return to any pre-existing conditions.

Conclusions

That ecologic conditions in the southwestern United States during the Pleistocene have varied considerably from those characteristic of the same region today can hardly be doubted. It is impossible to reconcile the tolerances and habitat preferences of many narrowly adaptable mammals living here in the past with the essentially hostile climate and environment of the same region at present. The occurrence of essentially boreal mammals in deposits as far south as southern Texas and Mexico is an incongruity that can be explained satisfactorily only by inferring climatic change. Hibbard (1955) and Cushing (1945), in discussing the presence of *Synaptomys cooperi* in deposits of San Josecito Cave, Nuevo Leon, Mexico, suggest that its distribution far to the south was controlled by the development of tall-grass areas. Hibbard (1955, p. 83) states that *Pitymys* (pine vole) and *Synaptomys* "must have grazed their way into Mexico at a time when strips or areas of grassland existed where semiarid conditions prevail today. The animals advanced with changing cli-

matic conditions that supported the development of tall grasses and sedges." Evidence amassed by Blair (1958) and other workers suggests that these conditions were afforded by the effect of the southward extension of the continental ice sheet during Wisconsin time. Withdrawal of the ice sheet and consequent climatic shift would result in either extirpation of the more moist-adapted species from their former range or in stranding some of these forms as relict populations in locally favorable environments throughout northern Mexico and southwestern United States. Whether the fossils from Miller's Cave are remains of a fauna that lived in the area during a glacial age or whether they represent the last survivors of a glacial fauna that was stranded after retreat of the ice sheet cannot be absolutely determined. However, the abundance and diversity of the animals represented reflect not a waning, marginal environment, but one providing nearly optimal conditions of temperature, moisture, and other factors necessary for survival.

Summary

A study of fossil vertebrates evacuated from Miller's Cave, Llano County, Texas, indicates that climatic conditions in the Llano region during the time these animals lived differed

considerably from those obtaining in the same region today. Climatic inferences drawn from the study of fossil forms were made on the basis of distribution patterns and habitat pref-

erences of living members of the species group. Additional evidence is provided by physical analysis of the fossil-bearing sediment.

Evidence used in reaching these conclusions are summarized as follows:

1. The presence of great quantities of travertine in the highly fossiliferous unit. The accumulation of travertine is evidence of a general increase in regional moisture; its absence in the unit above indicates a shift towards an increasingly more arid regimen.

2. The presence of large, angular, breakdown boulders in the travertine unit. The product of rapid breakdown of the parent rock, they indicate an increase in the amount of water introduced into the cave complex, in turn reflecting a more moist climate.

3. The greater quantity of kaolinite found in soils comprising the travertine unit compared to that in soils of the brown clay unit. This suggests a more intense weathering process which gradually lessened from the time of travertine deposition to the present.

4. The changing patterns of distribution and associations of animals present in the fossil fauna. Several members of the fauna are now distributed far to the north and to the east of the Miller's Cave region. Others, whose extrapolated distribution patterns indicate their

presence in the region today, are not actually present but are found only in locally favorable habitats some distance away.

5. The ecological and physiological requirements of many of the individual members of the fossil fauna show that the climate of the Llano region must have been able to support the existence of permanent streams, marshes, or bogs, as well as the development of a deep, moist soil and rich grasslands.

The Llano region today is semiarid and is subject to long periods of drought. Permanent bodies of water are now rare and hygric vegetation is relatively sparse. The physical characters of the sediments described, as well as the narrow ecological tolerances of various elements of the fossil fauna, preclude the existence of such a climatic regimen at the time these animals lived. The combination of these factors indicate that climatic conditions were equable; rainfall was greater and more effective, and mean annual temperature was probably cooler with summer extremes much reduced.

Finally, fossil species also allow reconstruction of four different communities which contributed to the fauna: stream and marsh border community, lowland meadow community, shrub and tree community, and upland prairie community.

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